

THE DIGGING AND PROVISIONING BEHAVIOR OF
AMMOPHILA SAEVA SMITH

(Hymenoptera: Sphecidae)

J. W. TILDEN

*Department of Biological Science
San Jose State College, San Jose, Calif.*

During the summer of 1949 individuals of this species were found on the floor of Bixby Canyon, Monterey County, California, and the activities of the females were observed. According to William Donald Murray (personal communication) *Ammophila saeva* Smith is distinct from *A. procera* Dahlbom. It seems of interest therefore to record the behavior of *A. saeva* and to compare with that of *A. procera*. The habits of the two species are very similar; those of *A. saeva* seem not to have been recorded previously¹.

OBSERVATIONS ON AMMOPHILA SAEVA SMITH

On June 30 a female was seen digging in dry alluvial soil containing numerous small gravelly deposits. The soil was friable but somewhat firm, and in all subsequent cases where digging was noted, it was done in soil of this type. Natural consolidations were seldom chosen, but roadways, paths and abandoned campsites, where the activities of man had packed the earth, were favored by the wasps. Most of these areas were quite close to the stream. The light sediments at some distance from the stream seemed to be entirely unsuited to the activities of the insect.

The burrow was far advanced when first located. When the wasp went below it stayed for two to three seconds, returning with a load of material in its mandibles. It backed out, turned to the right, and deposited the earth about five inches away from the opening, then returned to the left and entered the hole head first. In each case the same movements were made. In a few instances it returned to the right instead of to the left, but in no case did this individual turn to the left in approaching the mound of excavated earth. These movements resulted in the execution of small circles on the ground: out to the right, back to the left.

The wasp ceased digging after twenty minutes and closed the

¹ ACKNOWLEDGMENTS—Special thanks are due to Dr. William Donald Murray for identification of the wasp, and for reference, without which no comparison of the habits of various species would have been possible. His help and encouragement are gratefully remembered. The determination of *Hilarella* and a reference to its biology are due to the kindness of Dr. Curtis W. Sabrosky.

opening with a small rock about one-half inch in diameter. The rock was straddled and seemed to be grasped mostly in the mandibles. It is not clear that the fore legs assisted in the process. After closing the opening, the wasp flew away. It had not returned in half an hour, so the burrow was investigated. The pile of removed earth measured three and one-half by two inches, but the boundaries were irregular. The rock closure was lifted and the hole below was found to be open.

Later the same day, the burrow was found sealed and with a small piece of wood covering the place where the opening had been. The area had been smoothed and the piece of wood looked like any number of others in the vicinity. If the site had not been marked by a small stake, it might not have been rediscovered by the observer. A second burrow had been dug about twenty inches from the first, and also covered, this time by two pebbles inserted deeply into the opening.

When by noon the next day (July 1) the wasp had not returned, the first burrow was dug out and found to be three and one-fourth inches deep and to extend more than six inches back from the opening. The diameter of the vertical part was between one-half and three-fourths inches, but irregular and varying because the wasp had gone around the larger pebbles. The chamber at the end of the horizontal portion was about two inches long and one inch in height. This chamber was the only part of the tunnel that had not been refilled, but dimensions in the rest were not difficult to take since the loose material lay at different angles than the original soil. The chamber was provisioned with a single larva of the sphingid moth, *Smerinthus cerisyi* Kirby, which was one and three-fourths inches in length. A single egg had been laid on the pleuron of the last segment just above the right side of the anal prolegs. The second burrow was also dug out and found to be similar in most respects, with allowances for the differences in the soil.

On July 3 a female, presumably the same one, was collected and on July 13 a male. No other specimens were taken although several were observed from time to time.

At noon on July 12, another female was seen working in the same area. By 3:15 p.m. she had nearly completed her burrow, to judge by the size of the excavation pile. She dug as had the other, by means of mandibles only, and carried the earth farther from

the opening, depositing it about seven inches from the hole. This seemed to be an individual character in these wasps, each having a characteristic carrying distance because of the size of the circle started upon leaving the opening with a load. Whereas the previous female had turned always to the right when carrying the earth, this one turned to the left and returned to the right. It was a "left-handed" individual.

As the wasp dug, small flies loitered around the opening. They were very agile and active. One only was taken; it was identified by Dr. Curtis Sabrosky of the United States National Museum as *Hilarella hilarella* (Zetterstedt) (Sarcophagidae). Dr. Sabrosky informs me that there are a number of related species with these habits and suggests that if more had been collected, other species might have been represented. Allen (1926) reviewed the species of these flies, and mentioned that J. B. Parker found they larviposit, the small larvae perhaps, being dropped into the mouth of the wasp's burrow. In one case eight maggots were reared from a caterpillar found in the burrow of *Sphex extrematata* var. *pictipennis* Walsh. He stated that M. R. Smith seemed to find that eggs were laid on the caterpillar before it was put in the burrow. (Since these flies, in common with many Sarcophagidae, have been observed to larviposit, it may be that small larvae rather than eggs were laid on the larvae.)

The wasp left the area at 3:51 p.m. without covering the opening. This individual never covered the burrow upon leaving it. At 4:14 p.m. it returned, made a sweeping flight around the area, investigated the vicinity of the burrow and began at once to dig. In every observed instance, returning females behaved in a similar fashion when returning without provisions. Returning empty-handed was by flight, and the burrow investigated prior to resumption of digging.

At 4:22 p.m. the wasp stayed below and did not come out again that evening. By this time the spot had become shaded and cool, and it was found on this and other occasions, that relatively high ground temperatures were necessary to the insect's activity. The wasp spent the night in the burrow, as was tested by placing a rather large rock over the opening. Next morning when the weather cleared, the rock was removed and the wasp came out and flew directly away.

The next day (July 13) was clear in the morning but fog rolled

in early in the day and no digging was noted. The wasp was seen to investigate the hole but instead of digging she ran along the ground to the edge of the nearby vegetation and rested in the dry grass, where she spent the night. It seemed a matter of circumstances whether the night was spent in the burrow or not. Both types of behavior were noted several times.

Duties prevented observations for three days, but on July 17 a female, presumably the same one, was observed covering a hole. The wasp scratched with the prothoracic legs in a circular motion, moving around the hole and throwing the dirt back between the other two pair of legs. Most of the covering was done by backing up to the opening. When the hole had been filled to somewhat above the surrounding level, a small rock was placed on the mound. In this instance no stone was used for tamping.

Without resting, the wasp began to investigate the surrounding area. After about ten minutes, she selected a spot some three inches from the previous site and began to dig. She apparently did not encounter any underground obstacles, since excavation was unusually rapid and seemingly complete in 72 minutes. She then flew away without covering the opening. She also turned to the left in digging, and this together with the habit of not covering the opening led to the assumption that it was the same individual as before. The day turned cold and the wasp did not return that evening.

It was 3:20 p.m. the following day (July 18) before further observations could be made. The wasp was not in evidence, and the hole was still open. The nearby covered hole was dug out; it contained a *Smerinthus* larva. No egg was found, and at the time it was supposed that it had been brushed off during the excavation, but observations by Criddle (1924) may place a different interpretation on the matter. He describes how a caterpillar of the related *Smerinthus geminatus* Say (*S. jamaicensis* Drury of the present lists) was buried by *Ammophila procera* on one day and exhumed the following day to be oviposited on.

After the caterpillar had been examined, both the dug out and the open hole were filled and the area smoothed, and the return of the wasp was awaited. She returned soon, at 3:31 p.m., dragging a large *Smerinthus* larva. The wasp was astride the larva, holding it near the head in the mandibles, and walking on all six widely-

spaced legs. The larva seemed not to be any great burden to the wasp, which moved rapidly and easily.

The wasp was disturbed to find no hole, and walked around the exact location of the now filled-in opening, still dragging the larva. Then she set the caterpillar down a short distance away and investigated the area most carefully, returning occasionally to re-examine the larva. After some ten minutes of these actions, the wasp selected a new site and began to excavate a new burrow. She dug very rapidly, making numerous loud buzzing sounds. Soon the burrow was deep enough so that the wasp was underground for several seconds, and during one of these trips the larva was removed and examined. No egg was found, so it seems that oviposition may occur after the larva is placed in the burrow. The larva was returned as nearly as possible to the same place.

At 4:12 the burrow was complete and the wasp took wing and flew several times in long low sweeps around the vicinity. She located the larva from the air, dropped to the ground beside it, resumed a position astride the larva and dragged it to the new burrow. She dropped the larva an inch or so from the mouth of the burrow and went down into the hole, returning with a load of earth. Two such trips were made. Then she backed into the opening, dragging the larva after her, not straddled, but seized in the mandibles. No egg was deposited at this time. The wasp remained below nearly three minutes, and when she returned to the surface was carrying more material. Several more trips were made, each with a load of earth. On one of these trips a large rock was placed over the opening by the observer, to prevent the wasp from coming out. She could be heard buzzing loudly below, but when the rock was removed continued her work without concern. This last excavation required eight minutes, and may have been a final cleaning out of the chamber.

Next the wasp retired a foot or so from the nest, and groomed her antennae for a short time. Then she began to gather pebbles about one-fourth inch in diameter and to dump them into the burrow. The observations at this time were made from about 18 inches without disturbing the wasp. The observer placed pebbles of an appropriate size near the opening and these were accepted and used. Small pebbles and larger rocks placed in the same way were examined, apparently being measured by the expanse of the mandibles, and discarded without being used.

When the hole was nearly full of pebbles, perhaps three-fourths of an inch from the top, the wasp began to fill the remainder with gravel and sand. As before, she faced away from the burrow and loosened the earth with her mandibles, then kicked it backwards with the prothoracic legs, the material passing between the other two pairs of legs and beneath the upraised abdomen. During this process, she stopped from time to time and seizing a small rock in her mandibles, carried it to the hole and used it to tamp the earth in the opening. The tamping was quite vigorous, the wasp raising the fore part of the body and beating the loose earth with a pushing motion. At the termination of each tamping act, the rock that had been used was either placed in the opening or laid beside it, while another layer was kicked in. Each time a different rock was used for the tamping. When the hole was slightly more than flush with the surface, a small rock was placed over the spot where the hole had been. Then the surrounding area was carefully smoothed. The filling of the hole with small material, including the use of the rocks as tools, took one minute and thirteen seconds.

The wasp then sought a sheltered and sunny location and groomed herself, after which she rested for nearly four minutes. She then began to search the vicinity, taking short flight and alighting repeatedly. However, no more excavation was done that day. The time was nearly five o'clock and day had become cool. The wasp flew away and did not return. The small *Hilarella* flies remained near the burrow during the entire process, even entering the hole while the wasp was below, but the wasp did not appear to notice them in any way. The caterpillar was then dug out but again, no egg was found.

Other excavations were observed on several occasions, without significant deviation from the patterns recorded above.

COMPARISON OF THE BEHAVIOR OF *AMMOPHILA SAEVA* WITH THAT OF *A. PROCERA* AND CERTAIN OTHER RELATED FORMS

The habits of certain species, mostly in eastern United States, have been recorded numerous times. Wheeler and Wheeler (1924) note the use of pebbles by these wasps in tamping the burrow, and state that seven observers have recorded this act since it was first described by Peckham and Peckham (1898). The Peckhams remarked that *A. urnaria* used the same pebble each time, so in this respect *A. saeva* differs, but such a difference may well be individual rather than specific.

Although the Wheelers credit the Peckhams with the first observation of the use of pebbles as tools by these wasps, two earlier records exist. Pergande (1892) observed the use of pebbles in this way by *A. gryphus* and stated that the tamping made audible sounds. Williston (1892) also recorded the use of pebbles by *A. yarrowi*. These seem to be the first published notes on this tool-using behavior by members of the genus *Ammophila*. The many later records indicate that it is most likely a usual habit.

All references consulted gave the provision of the burrow as lepidopterous larvae. Most of the references refer to the captured larvae as prey. But since the larvae are not eaten by the adult but used to supply food for the young, the term provision is preferable. In addition to the use of *Smerinthus* larvae (Criddle, 1924), Rau (1926) found that *A. procera* provisioned with a noctuid (phalaenid) larva. Hartman (1905) found that *A. procera* used a "tomato worm" (Sphingidae), and laid the egg on the 6th to 10th segment of the abdomen, while Pergande (1892) noted the utilization of the larva of *Heterocampa sub-albicans* Packard (Notodontidae).

Rau (1922) wrote that *A. procera* carried earth from the burrow in short flights, which is unlike the habits of *A. saeva*. Whether this is a real difference of behavior or merely a difference in description by two different authors, is not clear.

The specific names of the insects are given just as found in the literature without any attempt to bring them in line with modern classification, since the systematics of these insects is in no way part of this paper.

SUMMARY

Observations on *Ammophila saeva* Smith indicate that the wasp provisions the nest with the larva of *Smerinthus cerisyi* Kirby and uses pebbles to tamp the earth in the burrow. The habits of *A. saeva* are similar to or nearly identical with those of related species; the differences are slight enough to be individual and not specific. It would seem that the digging and provisioning habits of the genus *Ammophila* may be considered to form a generic rather than a specific habit pattern. Wheeler and Wheeler's statement that the Peckhams were the first to observe the use by these wasps of pebbles as tools is incorrect, since both Pergande and Williston made such observations earlier.

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NEW RECORDS OF OXYPORUS FROM ARIZONA (Coleoptera: Staphylinidae).—A specimen each of *Oxyporus quinque maculatus* Leconte and of *O. mexicanus* Fauvel were taken by the writer in the pine-Douglas fir forest at Rustler Park, Chiricahua Mountains, Arizona, on Sept. 15, 1952, at about 8,300 feet altitude. Five additional specimens of *O. mexicanus* labeled "Huachuca Mts., Carr Cn., Ariz., VIII-6-1924, J. O. Martin, Collector" are in the collection of the California Academy of Sciences, San Francisco. All these represent new records for the Southwest, *O. quinque maculatus* having been recorded previously from the eastern United States and *O. mexicanus* from Oaxaca in Mexico. For the latter species, these represent the first United States records. Since the species of *Oxyporus* are mushroom inhabiting forms, it may be assumed that *O. mexicanus* was found in the high mountains of Oaxaca where the fungi are likely to be present.—BORYS MALKIN, University of Washington, Seattle.